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COYOTE ACTIVITY PATTERNS IN THE SIERRA NEVADA

John A. Shivik[1,2], Michael M. Jaeger[3], and Reginald H. Barrett[1]

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The winter months in high mountain regions of the Sierra Nevada make survival difficult for predators that exist there. High productivity during the spring and summer enables coyotes (*Canis latrans*) to survive and reproduce, but little is known about how these animals overwinter in mountainous areas. Hawthorne (1970) suggested that coyotes make altitudinal migrations, but recent data (Gantz 1990, Gese et al. 1996, Shivik et al. 1996) indicate that coyotes can remain in the high mountains throughout the year.

Temporal rhythms (e.g., innate behavioral rhythms such as diel cycles and seasonal reproductive cycles) may influence, or help elucidate, coyote activity patterns. We hypothesized that coyotes vary activity levels throughout the year as a result of these seasonal biological requirements. We related coyote activity patterns to the seasons that are likely to influence these patterns. We analyzed coyote activity in the Sagehen Basin of the Sierra Nevada because seasonal activity patterns in this seasonally cold and snowy climate provide insight into how coyotes allocate energy in order to survive and reproduce.

Previous analyses of coyote activity used movement data to determine activity levels (Gipson and Sealander 1972, Andelt and Gipson 1979, Smith et al. 1981, Gese et al. 1989). However, some authors argued that using distance traveled is not a good measure of coyote activity (Knowlton et al. 1968, Laundré and Keller 1981). The literature presents a paucity of analyses examining seasonal trends in coyote activity using activity-sensitive collars (especially in mountainous areas). Therefore, we conducted a study using activity-sensitive radiocollars to monitor seasonal coyote activity in a mountainous region of the Sierra Nevada.

Materials and Methods

We conducted our research in the 105-km^2 watershed surrounding the University of California Sagehen Research Station, approximately 13 km north of Truckee, California, in the Tahoe National Forest. Elevation ranges from 1880 to 2620 m. The area is characterized by long, cold winters and warm, dry summers with nightly temperatures falling below 0°C, often at all times of year. Most of the annual precipitation (91 cm) falls as snow during winter. Forested areas are dominated by Jeffrey pine (*Pinus jeffreyi*) and white fir (*Abies concolor*). Brush fields contain deerbrush (*Ceanothus velutinus*) and greenleaf manzanita (*Arctostaphylos patula*). Sagebrush (*Artemisia tridentata*) dominates on lower, dry slopes. Small stands of lodgepole pine (*Pinus contorta* var. *murryana*) and aspen (*Populus tremuloides*) occur near springs, meadows, and streams. Red fir (*Abies magnifica*), mountain hemlock (*Tsuga mertensiana*), and western white pine (*Pinus monticola*) dominate at higher elevations (Morrison et al. 1985).

We trapped coyotes using steel leghold traps with offset, padded jaws and short anchor chains to minimize trapping injury and stress (Hawthorne 1970, Olsen et al. 1986). Coyotes were immobilized physically (with a pin-stick and then vet-wrap or electrical tape). The sex, weight, age (Gier 1968), and general condition were recorded for each captured coyote (Shivik 1995). During the course of the study, we made 18 captures of 16 coyotes during 3 trapping periods.

Radiocollars with signal-pulse varying activity switches (Model 400; Telonics, 932 E. Impala Ave., Mesa, AZ 85204-6699) were fitted to each coyote. These collars transmitted a 75 pulse/

[1]Department of Environmental Science, Policy and Management, 151 Hilgard Hall, University of California, Berkeley, CA 94720.
[2]Present address: Department of Biology, Colorado State University, Fort Collins, CO 80523.
[3]USDA National Wildlife Research Center, 151 Hilgard Hall, University of California, Berkeley, CA 94720.

min signal when the collar was moving and a 50 pulse/min signal when it was stationary for over 1 min. Hand testing of the collars indicated that the internal switches were quite sensitive and that a very small amount of movement was required to set the collar into "active" mode. Therefore, for purposes of this study, a nonactive coyote was one that had not moved for over 1 min (and was probably sleeping).

Concurrent with attempts to locate each animal, we monitored collared coyotes for activity during eight 4-hr radio-tracking sessions per week (Shivik et al. 1996). Coyotes were monitored once per hour in 4-hr blocks that bracketed sunrise, middle of the day, sunset, and middle of the night. Each coyote was monitored for approximately 2 min each hour during the 4-hr tracking session. For analysis, data were divided into the following 6-hr categories: "morning" (>0400 and ≤1000), "day" (>1000 and ≤1600), "evening" (>1600 and ≤2200) and "night"(>2200 and ≤0400). A coyote's percent activity during each block was the basic dependent variable. We calculated the estimate of percent activity by dividing the number of times the animal was recorded as active by the total number of times it was heard during the block of monitoring if the number of samples was ≥2.

The influence of seasonal factors, such as weather patterns, cannot be easily separated from changes due to internally controlled behavioral rhythms. However, to survive and reproduce, coyotes must pursue certain behaviors (e.g., forming pair bonds, maintaining territories, and feeding pups) regardless of environmental conditions. Therefore, we used the biological season as the basis for examining coyote activity through time (Laundré and Keller 1981, Smith et al. 1981). Data were divided into the following seasons for analysis: breeding (1 January–15 March), pre-pup (16 March–30 April), pup rearing (1 May–31 July), and dispersal (1 August–31 December). Data were collected 1 August 1993–31 July 1994.

We assessed activity levels by animal within seasons during the regularly scheduled morning, evening, midday, and midnight tracking sessions, and arcsine transformed the activity rate for each coyote before analysis (Zar 1984). Because seasonal activity could be influenced by the sex of the coyote, we analyzed data using a 2-way ANOVA. We hypothesized differences in activity between sex and season and also used ANOVA to determine whether differences in activity were apparent at different times of day during the biological seasons.

For all analyses, the sample unit was the individual coyote. For example, in the ANOVA of the percent activity by season and day category, all activities of coyote F040 during each season and day category were reduced to a single average to avoid pseudoreplication (Hurlbert 1984). If a significant difference in mean activity level was detected, we performed multiple comparisons using Tukey tests. Statistical assumptions were assessed using residual plots (Kirby 1993).

RESULTS AND DISCUSSION

For the 12 coyotes (7 males and 5 females) monitored, 1368 activity rates were calculated for the 4 time-of-day categories ($\bar{x}$ = 342 per season, $\bar{x}$ = 114 per coyote) from 2150 observations on individual coyotes ($\bar{x}$ = 538 per season). Mean activity varied between seasons ($P < 0.001$), but there was no evidence for a difference in activity by sex ($P = 0.63$) and no interaction between sex and season ($P = 0.192$). Because we did not detect a difference in activity between sexes, we did not partition out the effects of sex in the remaining analyses. Coyote activity during the breeding season was significantly less than the pup ($P < 0.001$) and dispersal ($P = 0.011$) seasons, and activity was less during the pre-pup than the pup ($P = 0.029$) season (Fig. 1). Activity significantly varied by day category only during the dispersal season ($P = 0.033$) when activity peaked during the evening ($\bar{x} = 0.60$, $s_{\bar{x}} = 0.05$) and was lowest during the day ($\bar{x} = 0.42$, $s_{\bar{x}} = 0.04$).

Our results are consistent with those of other researchers who found that coyote activity varied by time of day, even when previous studies used different methods to rate activity and involved different degrees of pseudoreplication (Gipson and Sealander 1972, Andelt and Gipson 1979, Shivik and Crabtree 1995). Furthermore, other studies did not show differences in activity between males and females (Gipson and Sealander 1972, Andelt and Gipson 1979), suggesting that activity rates of males and females do not differ drastically. However, Laundré and Keller (1981) indicated that females travel less than males during the pup season, leading us to hypothesize that,

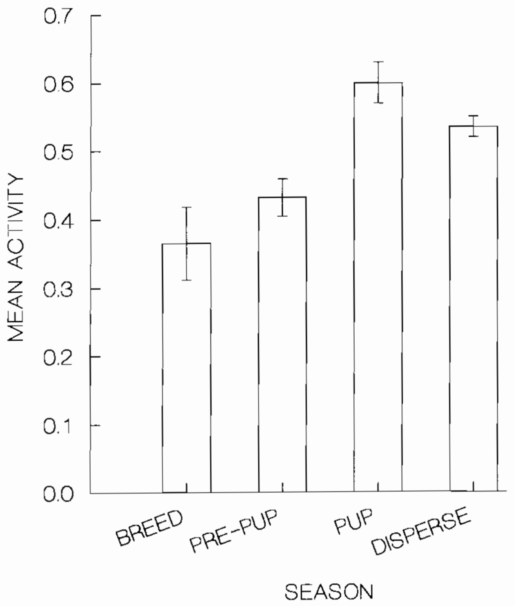

Fig. 1. Seasonal activity of coyotes in the Sagehen Basin of the Sierra Nevada. Bars represent 1 standard error. Means were calculated using each coyote as the sample unit after estimating individual coyote activity within each season. The breeding season was 1 January–15 March (n = 7), pre-pup was 16 March–30 April (n = 7), pup was 1 May–31 July (n = 11), and dispersal was 1 August–31 December (n = 12).

overall, female activity is not reduced but that travel by female coyotes is limited to a smaller area during the pup season. Differences between what the distance traveled metric and absolute activity measure actually represent contribute to confusion regarding seasonal changes in coyote activity (Lanudré and Keller 1984). Female coyotes that are nursing pups would be considered active by our method and not active when using distance-traveled data. A correlation is evident, however, between distance traveled and absolute activity, and therefore both distance traveled and motion-sensitive radiocollar data are useful for examining diel and seasonal coyote activity, noting that each method is sensitive to different behaviors.

Coyotes in Grand Teton National Park rest more during winter months because coyote reliance on carrion reduces the need to hunt small mammal prey (Bekoff and Wells 1980). Similarly, in Yellowstone National Park, coyotes reduce activity as available carcass biomass increases (Gese et al. 1996). During our study coyotes were also less active during winter (breeding and pre-pup seasons), but because deer are absent from this study area in winter, the carcass mechanism for decreased activity proposed by Bekoff and Wells (1980) may not apply to Sagehen coyotes.

The ultimate mechanism for reducing energy expenditures during winter may be that reduced winter activity probably improves chances for individual survival. Because activities such as pup rearing are not occurring, coyotes are able to reduce their levels of activity during winter. This behavioral plasticity allows coyotes to survive and reproduce in mountainous areas, even when carrion (e.g., from winter-kill ungulates) is not available. Thus, the proper currency for examining coyote ability to remain in areas with a seasonally reduced prey base and harsh weather conditions is the amount of time relegated to social and reproductive behaviors. In seasons when activity-intensive behaviors such as pup rearing are not occurring, coyotes reduce energy expenditures and exist in areas with seasonally limited food supplies.

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